

THE ANALYSIS OF A CATCH CURVE

D. S. Robson

BU-113-M

Cornell University

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INTRODUCTION. The analysis of a catch curve, or the age-frequency distribution of the catch, to obtain information on the vital statistics of a fish population goes back at least to 1908 when Edser [1] published catch curves for plaice of the North Sea. The earlier users worked with age indirectly, using some correlated variable such as body length to separate the catch approximately into age groups. Today, however, improved aging techniques such as scale reading make it possible to work directly with age in most studies.

When plotted graphically, the age-frequency distribution in a population typically presents a staircase appearance, descending with increasing age, and with the height of the steps steadily decreasing. The basic idea underlying catch curve analysis is that the drop in frequency from one age group to the next reflects the combined effect of mortality and the differences in initial year class strength for the two age groups. The amount and kind of information which can be extracted from a catch curve, however, depends upon the amount and kind of information which the investigator can put into the underlying models of the population and the sampling process -- or depends, in other words, upon the type of simplifying assumptions which can be reasonably made concerning the population and the sampling process. The user may, for example, acknowledge that his sampling gear is selective against younger fish, but may consider it reasonable to assume that beyond some minimum age all fish are equally vulnerable to the gear employed. Information concerning the relative year class strengths and survival rates may be available from other sources, either direct information from previous studies on this same population or indirectly from the results of studies on similar populations.

If no simplifying assumptions concerning the population can be made, if year classes must be acknowledged to vary in strength and survival rates to vary from year class to year class and age to age then the age-frequency distribution in the catch of a single season provides no identifiable information whatsoever regarding these unknown population parameters. In order to separate the effects of mortality from the effects of variable year class strength it then becomes necessary to obtain catches over a series of years, and either provide that the expected average catch per unit of effort remains each year in constant proportion to total abundance, or to supplement -- or even replace -- the catch curve analysis with a

tag-recapture program.

The theory of catch curve analysis, however, should logically begin with the simpler problem of a single catch curve and a simplified population and sampling model. The present paper will be concerned exclusively with this simple and classical problem in which year class strength and annual survival rates are assumed to be constant, at least over a limited range of age groups, in which case the problem reduces simply to examining methods of estimating the constant but unknown annual survival rate. Included in our discussion, however, are several methods for testing these basic, simplifying assumptions.

METHODS OF ANALYSIS WHEN AGE IS KNOWN EXACTLY FOR ENTIRE SAMPLE. Chapman and Robson [2] have shown that unbiased estimates of annual survival rate may be derived from the catch curve for a single season if the assumptions of constant year class strength and survival rate hold true and if all fish beyond some minimum age are equally vulnerable to the sampling gear. Furthermore, among the many possible unbiased estimators which exist in this case, there is one which is uniquely best in the sense that it is subject to the smallest amount of sampling error. To illustrate the form of this and other analytic procedures we shall employ the age-frequency distribution in a sample of 243 rock bass of age VI⁺ and older, trap-netted from Cayuga Lake, New York, during a single summer season. For the present purposes, VI⁺ was arbitrarily chosen to represent the youngest age group fully vulnerable to trap-netting. The age composition of this catch is shown in the age-frequency table below, with age VI⁺ coded back to 0:

Age	VI ⁺	VII ⁺	VIII ⁺	IX ⁺	X ⁺	XI ⁺	Total
Coded age	0	1	2	3	4	5	Sample size
Number in catch	N ₀ =118	N ₁ =73	N ₂ =36	N ₃ =14	N ₄ =1	N ₅ =1	n=243

The best estimate of the assumed constant annual survival rate is based upon the total or mean coded age in the sample. If T denotes total and n denotes sample size then here

$$\begin{aligned}
 T &= N_1 + 2N_2 + 3N_3 + \dots \\
 &= 73 + 2(36) + 3(14) + 4(1) + 5(1) \\
 &= 196
 \end{aligned}$$

and

$$\begin{aligned} n &= N_0 + N_1 + N_2 + \dots \\ &= 118 + 73 + 36 + 14 + 1 + 1 \\ &= 243 \end{aligned}$$

The best estimate of survival rate is then computed from the formula

$$\begin{aligned} \text{annual survival rate estimate} &= \frac{T}{n+T-1} \\ &= \frac{196}{196+243-1} \\ &= .4475 \end{aligned}$$

If the true annual survival rate in the population is s then among samples of size n the average value of this estimator will be exactly s , and the variance about this average value will be

$$\text{variance of estimate} = \frac{s(1-s)^2}{n}$$

Since the variance of the estimate depends upon the unknown true survival rate s then the variance, likewise, is unknown and must be estimated from the sample, and is therefore also subject to sampling error. The best estimate of the variance, best in the sense of being unbiased and subject to the smallest possible sampling error, is given by

$$\begin{aligned} \text{estimate of variance} &= \frac{T}{n+T-1} \left(\frac{T}{n+T-1} - \frac{T-1}{n+T-2} \right) \\ &= \frac{196}{438} \left(\frac{196}{438} - \frac{195}{437} \right) \\ &= .000566 \end{aligned}$$

The standard error, or square root of the variance, is therefore estimated by

$$\text{standard error} = \sqrt{.000566} = .0238$$

Since the sampling distribution of the survival rate estimate approaches the normal distribution as sample size gets large, approximate 95% confidence intervals on the survival rate are given by

survival rate - 2(standard error) < s < survival rate + 2(standard error)

or

$$.4475 - 2(.0238) = .40 < s < .50 = .4475 + 2(.0238) .$$

Thus, one could state with (95%) confidence that if year class size and survival rates are actually constant in this rock bass population then the true annual survival rate falls somewhere between 40% and 50%, the best point estimate being 45%.

Other estimates exist which are unbiased if the simplifying assumptions of the model are true, and differences between alternative unbiased estimates may in fact be used as criteria to test the validity of the simplified model. One such alternative estimate especially suited to this purpose is Heincke's [3] estimate of survival rate, $(n-N_0)/n$. This is essentially the same as Jackson's [4] estimate $(n-N_0)/(n-N_k)$, where N_k is the number of fish in the oldest age group occurring in the sample and is usually a small number relative to the total sample size n and to the number N_0 occurring in the youngest age group. Insofar as Heincke's and Jackson's estimates do differ, Heincke's is the better in this case, being unbiased and subject to the smaller sampling error. For the data used here, Heincke's estimate becomes

$$\frac{n-N_0}{n} = \frac{243-118}{243} = \frac{125}{243} = .5144$$

When a discrepancy arises between Heincke's estimate and the best estimate it may be attributed directly to a discrepancy in the 0 age group frequency relative to the frequencies in the older age groups. In the present case, Heincke's estimate exceeds the value .4475 obtained for the best estimate, implying a deficit in the 0 group relative to the older age groups. The test of whether this observed discrepancy may be attributed to sampling error or must be considered as real takes the form of a chi-square test,

$$\begin{aligned} \text{chi-square with 1 d.f.} &= \frac{(\text{Best est.} - \text{Heincke's est.})^2}{T(T-1)(n-1)/n(n+T-1)^2(n+T-2)} \\ &= \frac{(.4475 - .5144)^2}{196(195)(242)/243(438)^2(437)} \\ &= 9.858 > 3.841 \end{aligned}$$

Since chi-square values in excess of 3.841 arise only 5% of the time when the discrepancies are due solely to sampling errors, we must in this case reject the hypothesis that our observed discrepancy is a result of sampling error. Our conclusion must therefore be that the fault lies with the basic model which implied that these estimates should differ only by sampling error. The fault may lie in the assumption of constant year class size or in the assumption of constant survival rate or in the assumption of equal vulnerability of all age groups to the sampling gear. The chi-square test cannot discriminate between the possible causes of the failure of the model, but merely establishes whether or not reasonable agreement exists between the observed frequency in age group 0 and the frequency expected on the basis of the data in the older age groups.

An exactly analogous test procedure may be applied to age group 1 simply by eliminating age group 0 from the data, recoding, and then applying the above formulas to the reduced data. Upon eliminating age 0 and then recoding we obtain for this example:

Age	VII ⁺	VIII ⁺	IX ⁺	X ⁺	XI ⁺	Total
Recoded age	0	1	2	3	4	sample size
Number	73	36	14	1	1	125

The new total T then becomes

$$T = 36 + 2(14) + 3(1) + 4(1) = 71$$

and with n=125 the best estimate of survival rate is

$$\frac{T}{n+T-1} = \frac{71}{125+71-1} = .3641$$

The new N_0 is 73, so Heincke's estimate for this reduced data is

$$\frac{n-N_0}{n} = \frac{125-73}{125} = .4160$$

Again, the discrepancy between the two estimates is in the direction which implies a deficiency in the youngest age group, and chi-square value

$$\frac{(\text{Best est.} - \text{Heincke's est.})^2}{T(T-1)(n-1)/n(n+T-1)^2(n+T-2)} = \frac{(.3641 - .4160)^2}{71(70)(124)/125(195)^2(194)} = 4.032$$

shows this deficiency in age VII⁺ to be significant.

This process may be continued by starting the age-frequency table with age VIII⁺ as the 0-group, and in this example the resulting chi-square value was non-significant. With rock bass, selectivity of the trap net for larger and therefore older fish cannot be ruled out as a possible explanation of the observed deficiencies in ages even as great as VI⁺ and VII⁺.

METHODS OF ANALYSIS WHEN SOME OF THE AGE GROUPS ARE COMBINED. Thus far we have assumed that when the simplified model does hold true, the only error in the estimate is the random error associated with the sampling process. In practice, another source of error variation is the process of measuring age; two independent age determinations on the same fish specimen do not always yield the same result. With such commonly used procedures as scale- or otolith-reading the difficulty of age determination and the frequency of aging errors increases with the age of the fish. One way to alleviate this difficulty and at the same time eliminate the majority of the aging errors is simply to attempt exact aging only for the younger agegroups, and combine all of the remaining age groups together. This technique clearly sacrifices some of the potential information contained in the sample; on the other hand, the greater ease of operation may permit the use of larger samples to compensate for this loss. It would seem worthwhile, therefore, to investigate the estimation problem and the loss in statistical efficiency associated with this technique.

In general, if fish up through K years of age are all aged exactly and all fish K+1 years old or older are grouped together then the tabulated age frequency distribution will take the form:

Coded age	0	1	2	...	K	K+1 or older	Total sample size
Number in catch	N ₀	N ₁	N ₂		N _K	m	n

The best (maximum likelihood) estimate of annual survival rate in this case depends on the total T and the sample size n

$$T = N_1 + 2N_2 + 3N_3 + \dots + KN_K + m(K+1)$$

$$n = N_0 + N_1 + N_2 + \dots + N_K + m$$

and takes the form

$$\text{annual survival rate estimate} = \frac{T}{n-m+T}$$

The variance of this estimate, under the assumption that no errors are committed in this modified age classification technique, is

$$\text{variance of estimate} = \frac{s(1-s)^2}{n(1-s^{K+1})}$$

where s is again the true survival rate in the population being sampled. The efficiency of this technique relative to aging all fish exactly is therefore $100(1-s^{K+1})\%$; in other words, to obtain the same accuracy by this method as is obtained by aging all fish exactly, the present method would require $100/(1-s^{K+1})$ fish for every 100 fish used in the old method. Table 1 shows the numerical value of this relation for several values of s and K , and it is apparent that with

Table 1. Sample size required to obtain precision equal to that of a sample of 100 in which all fish are aged exactly.

<u>Ages grouped together</u>	True annual survival rate in the population		
	<u>.25</u>	<u>.50</u>	<u>.75</u>
1 and older	133	200	400
2 and older	107	133	228
3 and older	101	114	173
4 and older	100	107	146
5 and older	100	103	132
6 and older	100	101	122
⋮	⋮	⋮	⋮
all aged exactly	100	100	100

survival rates in the neighborhood of .50, which commonly occur in practice, little would be gained by attempting exact aging on more than the first two or three age groups if this method of estimation is to be employed.

The numerical computation of this survival rate estimate for the rock bass data has already been illustrated for the case $K=0$, since in this case the estimate reduces to the unbiased estimate proposed by Heincke. As another example,

if all rock bass of age IX⁺ and older were grouped together,

Age	VI ⁺	VII ⁺	VIII ⁺	IX ⁺ and older	Total
Coded age	0	1	2	3 and older	sample size
Number in catch	118	73	36	16	243

the estimate of survival rate would be

$$T = 73 + 2(36) + 3(16) = 193$$

$$n = 118 + 73 + 36 + 16 = 243$$

$$m = 16$$

$$\frac{T}{n-m+T} = \frac{193}{243-16+193} = \frac{193}{420} = .46$$

compared to the value .45 obtained when all age groups were held separate. The variance of the estimate would, in turn, be estimated by applying this estimate of s to the variance formula $s(1-s)^2/n(1-s^3)$,

$$\frac{.46(1-.46)^2}{243[1-(.46)^3]} = .000612$$

As expected, this is only slightly larger than the value .000566 obtained earlier for the case where all fish were aged exactly.

METHODS OF ANALYZING A SEGMENT OF THE CATCH CURVE. Circumstances frequently arise which make it necessary to truncate the catch curve on the right as well as the left. The sampling gear, for example, may be effective only for a limited range of fish size and therefore age so that different gear is used for each of several size classes, and these different pieces of gear may operate at different levels of efficiency. Or the exploitation of the fishery may be differentially selective for different size classes, thus precluding a constant survival rate. Such circumstances lead to a partitioning of the catch curve into segments and a separate analysis on each segment, so we shall consider now methods of analyzing a segment of a catch curve.

Following the notation of the preceding section, we may denote the age groups within a segment as ranging from 0 to K on the coded scale,

Coded age	0	1	2	...	K	Total number
Number in catch	N_0	N_1	N_2	...	N_K	n

The annual survival rate, which is assumed to be constant for this set of age groups in the population is then estimated as the solution to the equation

$$\frac{T_K}{n} = \bar{x}_K = \frac{s}{1-s} - (K+1) \frac{s^{K+1}}{1-s^{K+1}}$$

where

$$T_K = N_1 + 2N_2 + 3N_3 + \dots + KN_K$$

$$n = N_0 + N_1 + N_2 + \dots + N_K$$

and $\bar{x}_K = T_K/n$ is the average coded age in this segment of the sample. For $K=1$, i.e., for a segment of two adjacent age groups, this solution is

$$s = \frac{\bar{x}_1}{1-\bar{x}_1} = \frac{N_1}{N_0}$$

and for $K=2$, or the case of three consecutive age groups in a segment the solution is

$$s = \frac{-(1-\bar{x}_2) + \sqrt{1+6\bar{x}_2-3\bar{x}_2^2}}{2(2-\bar{x}_2)}$$

For larger values of K the solution must be obtained iteratively, and table 2 is provided to facilitate this iteration process as illustrated by the following example:

Coded age	0	1	2	3	Total number
Number	118	73	36	14	241

$$\bar{x}_3 = \frac{73+2(36)+3(14)}{241} = \frac{187}{241} = .775934$$

Entering table 2 with $K=3$ we find that if \bar{x}_3 were .733333 the solution would be $s=.50$ and if \bar{x}_3 were .819330 the solution would be $s=.55$. Linear interpolation gives

$$s = .50 + \frac{.819330-.775934}{.819330-.733333} (.05) = .50 + \frac{.043396}{.085997} (.05) = .5252$$

and substituting this value of \underline{s} into the equation

$$\bar{x}_3 = \frac{s}{1-s} - 4 \frac{s^4}{1-s^4}$$

gives

$$.7759 = \frac{.5252}{1-.5252} - 4 \frac{(.5252)^4}{1-(.5252)^4} = .7768$$

The fact of the right hand side being greater than the left implies that linear interpolation led to overestimation of s ; if we reduce the value of s from .5252 to .5250 we find somewhat better agreement,

$$\frac{.525}{1-.525} - 4 \frac{(.525)^4}{1-(.525)^4} = .7763$$

but the estimate is still slightly too large. Reducing to .5248 we find

$$\frac{.5248}{1-.5248} - 4 \frac{(.5248)^4}{1-(.5248)^4} = .7761$$

Clearly, the solution to three decimal places is $\underline{s}=.525$.

The variance of the estimate obtained from a segment consisting of $K+1$ consecutive age groups is given by the formula

$$\text{variance of estimate} = \frac{1}{n} \left[\frac{1}{s(1-s)^2} - \frac{(K+1)^2 s^{K-1}}{(1-s^{K+1})^2} \right]$$

so in the present case with $K=3$ the estimate of variance is

$$\frac{1}{241} \left[\frac{1}{.525(1-.525)^2} - \frac{16(.525)^2}{(1-(.525)^4)^2} \right] = \frac{1}{241} [8.4422 - 5.1649] = .001266$$

The precision of estimation from a segment of the catch curve is substantially less than the precision obtained from using the entire catch curve; the above variance estimate is more than twice as large as the variance estimate of .000566 obtained using the complete catch curve. In fact when the true survival rate in the population is .50 for all age groups then the efficiency of using just the first four age groups relative to using all age groups to estimate survival rate is only .43%. As mentioned earlier, however, circumstances do arise where it is

necessary to estimate survival rate separately for different segments of the catch curve.

A test of the validity of the simplified model is also possible using just the data for three consecutive age groups. The test criterion is again a chi-square measure of the departure of the observed from the expected frequency in the coded age 0 group, where the expected frequency is computed under the assumptions of constant year class size, constant survival rate, and equal vulnerability to sampling gear for the three age groups. Numerical values ϕ_n for the expected frequency in age group 0 are given in Table 3, and may be compared to the observed frequency N_0 by means of the chi-square formula

$$\text{chi-square with 1 d.f.} = \frac{(N_0 - \phi_n)^2}{\phi_n(\phi_{n-1} + 1 - \phi_n)}$$

Table 3 is entered in column $n=N_0+N_1+N_2$ and row $T=N_1+2N_2$; if T is greater than n then the table is entered in row $T=N_1+2N_0$ and in the chi-square formula N_0 is replaced by N_2 .

To illustrate this test we apply it to age groups VIII⁺, XI⁺ and X⁺ of the rock bass sample:

Age	VIII ⁺	IX ⁺	X ⁺	Total
Coded age	0	1	2	number
Number	$N_0=36$	$N_1=14$	$N_2=1$	$n=51$

$$T = N_1 + 2N_2 = 14 + 2(1) = 16$$

From table 3, for $T=16$ we find

$$\phi_{51} = 37.7483 \qquad \phi_{50} = 36.7830$$

so

$$\text{chi-square} = \frac{(36-37.7483)^2}{37.7483(37.7830-37.7483)} = 2.333$$

and since this chi-square value is less than the critical value of 3.841 we cannot reject the validity of the simplified model. This result is consistent with the conclusion drawn earlier that the deficiency in age group VIII⁺ relative to all older age groups is not statistically significant.

Table 2

$$Z_k(s) = \frac{\sum_{t=1}^k ts^t}{\sum_{t=0}^k s^t}$$

s	k=2	k=3	k=4	k=5	k=6	k=7
0.05	0.052256	0.052607	0.052630	0.052632	0.052632	0.052632
0.10	0.108108	0.110711	0.111061	0.111105	0.111110	0.111111
0.15	0.166311	0.174445	0.176091	0.176398	0.176459	0.176468
0.20	0.225866	0.243590	0.248399	0.249616	0.249910	0.249980
0.25	0.285714	0.317647	0.328446	0.331867	0.339206	0.333211
0.30	0.345324	0.395907	0.416392	0.424194	0.427040	0.428046
0.35	0.404075	0.477522	0.512062	0.527411	0.533955	0.536659
0.40	0.461538	0.561576	0.614937	0.641990	0.655179	0.661421
0.45	0.417398	0.647143	0.724183	0.767942	0.791927	0.804707
0.50	0.571429	0.733333	0.838710	0.904762	0.944882	0.968628
0.55	0.623482	0.819330	0.957244	1.051410	1.114003	1.154670
0.60	0.673469	0.904412	1.078418	1.206364	1.298401	1.363335
0.65	0.721351	1.030151	1.281308	1.455075	1.589050	1.690779
0.70	0.767123	1.069483	1.323212	1.533318	1.705117	1.843937
0.75	0.810811	1.148571	1.444302	1.700920	1.921673	2.109996
0.80	0.852459	1.224932	1.563065	1.868332	2.142434	2.387248
0.85	0.892128	1.298356	1.678625	2.033536	2.363805	2.670247
0.90	0.929889	1.368712	1.790286	2.194782	2.582407	2.953399
0.95	0.965319	1.435931	1.897530	2.350637	2.795275	3.231475
1.00	1.0	1.5	2.0	2.5	3.0	3.5

Table 3. Tabulated values of ϕ_n =the expected number in the youngest of 3 adjacent age groups when the total number in the 3 groups is n and the sum of the number in the second group plus twice the number in the third group¹ is t. Departure from expected is tested by chi-square with 1 degree of freedom:

$$\chi^2 = \frac{(\text{Observed number in youngest age group} - \phi_n)^2}{\phi_n(\phi_{n-1} + 1 - \phi_n)} \quad (\chi^2_{.05} = 3.841)$$

t	n=5	n=6	n=7	n=8	n=9	n=10	n=11	n=12	n=13
1	4.0000	5.0000	6.0000	7.0000	8.0000	9.0000	10.0000	11.0000	12.0000
2	3.3333	4.2357	5.2500	6.2222	7.2000	8.1818	9.1667	10.1538	11.1429
3	2.6667	3.6000	4.5454	5.5000	6.4615	7.4236	8.4000	9.3750	10.3529
4	2.1010	3.0000	3.9130	4.8421	5.7826	6.7317	7.6875	8.6486	9.6142
5	1.5686	2.4286	3.3158	4.2222	5.1429	6.0744	7.0145	7.9615	8.9143
6	1.1010	1.9149	2.7647	3.6429	4.5405	5.4526	6.3758	7.3079	8.2472
7		1.4286	2.2443	3.0945	3.9688	4.8608	5.7664	6.6829	7.6082
8			1.7647	2.5799	3.4272	4.2971	5.1839	6.0839	6.9946
9				2.0945	2.9130	3.7593	4.6260	5.5087	6.4039
10					2.4272	3.2470	4.0919	4.9558	5.8348
11						2.7593	3.5805	4.4245	5.2861
12							3.0919	3.9141	4.7572
13								3.4245	4.2476
14									3.7572
	n=14	n=15	n=16	n=17	n=18	n=19	n=20	n=21	n=22
1	13.0000	14.0000	15.0000	16.0000	17.0000	18.0000	19.0000	20.0000	21.0000
2	12.1333	13.1250	14.1176	15.1111	16.1053	17.1000	18.0952	19.0910	20.0870
3	11.3333	12.3158	13.3000	14.2857	15.2727	16.2609	17.2500	18.2400	19.2308
4	10.5833	11.5556	12.5304	13.5075	14.4865	15.4672	16.4494	17.4330	18.4177
5	9.8718	10.8333	11.7983	12.7663	13.7368	14.7097	15.6845	16.6612	17.6394
6	9.1925	10.1429	11.0976	12.0560	13.0177	13.9823	14.9494	15.9188	16.8902
7	8.5409	9.4797	10.4237	11.3723	12.3249	13.2809	14.2400	15.2018	16.1661
8	7.9140	8.8407	9.7738	10.7122	11.6552	12.6024	13.5533	14.5073	15.4643
9	7.3095	8.2238	9.1453	10.0732	11.0065	11.9446	12.8869	13.8330	14.7824
10	6.7259	7.6271	8.5368	9.4537	10.3770	11.3057	12.2392	13.1771	14.1187
11	6.1620	7.0495	7.9468	8.8524	9.7652	10.6842	11.6087	12.5381	13.4719
12	5.6169	6.4900	7.3744	8.2681	9.1701	10.0791	10.9944	11.9150	12.8406
13	5.0900	5.9480	6.8187	7.7002	8.5909	9.4896	10.3952	11.3069	12.2241
14	4.5811	5.4229	6.2793	7.1480	8.0269	8.9149	9.8105	10.7130	11.6215
15	4.0900	4.9146	5.7559	6.6109	7.4777	8.3544	9.2397	10.1327	11.0323
16		4.4229	5.2481	6.0888	6.9427	7.8073	8.6824	9.5655	10.4559
17			4.7559	5.5815	6.4219	7.2747	8.1382	9.0110	9.8919
18				5.0888	5.9149	6.7549	7.6068	8.4689	9.3400
19					5.4219	6.2484	7.0880	7.9390	8.7998
20						5.7549	6.5818	7.4211	8.2713
21							6.0880	6.9152	7.7543
22								6.4211	7.2486
23									6.7543

¹ If the indicated sum exceeds n then enter the table with t=sum of number in second group plus twice the number in the first group, and use the observed number in the oldest age group in the chi-square test.

Condition	Control (○)	Mild (●)	Severe (□)
1	65	65	65
2	75	75	75
3	85	80	75
4	90	85	80
5	95	90	85

[illegible]

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